

NOTES ON THE BEHAVIOR OF BURYING BEETLES (NICROPHORUS SPP.)

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For several summers, ending with the season of 1928, the senior author had observed species of *Nicrophorus* (Coleoptera, Staphylinidæ, Silphinæ) burying small carcasses at Irondale (Haliburton County), Ontario, Canada, in July. Some of his observations were published (Milne, 1928). Much more extensive and detailed studies of burying beetles were made by Pukowski (1933) in Europe and Leech (1935) in British Columbia. These authors followed the life history from the time of burial, while the adults cared for the young, through the three instars of larval life, the prepupal and pupal periods, and made observations on emergence and feeding of the adults. Difficulty was reported in observing the burying behavior because of its nocturnal nature and because *Nicrophorus* was not abundant enough to justify the risks of disturbing beetles at work. Since the burying activities had been watched repeatedly in daylight at Irondale, the present authors made a return trip there in the summer of 1944, to prepare a Kodachrome motion picture of the burying beetles in their work above ground. Although the time available during the brief vacation from war research greatly restricted the experimental studies, it was possible to make further observations which extend and clarify the behavior of these insects.

1. SPECIES INVOLVED AT IRONDALE

Six species of *Nicrophorus* have been collected at carrion in this region by the authors, namely *N. sayi* Lap., *N. orbicollis* Say, *N. marginatus* Fab., *N. pustulatus* Hersch., *N. vespilloides* Hbst., and *N. tomentosus* Web. All these are easily distinguished in the field. Only *tomentosus* has the pronotum covered with yellow, appressed hair (which often becomes abraded on the two convexities of the disc). Only *sayi* and *marginatus* have distinctly curved hind tibiae. Only *vespilloides* and *tomentosus*

have the antennal clubs entirely black, the other species having at least part of the club orange red; these two species are also considerably smaller in average size. *Sayi* and *orbicollis* are very similar in markings, with the elytra mostly black, but with orange red in a sub-basal, irregular crossbar and a subapical spot. *Marginatus*, *vespilloides* and *tomentosus* are similar in markings, the elytra being mostly orange red, the bands of color continuing across both elytra, sometimes confluent also along the outer margins. *Pustulatus* is unique among these six species in having the pronotum transversely oval, the others having a circular disc; it also has the sub-basal elytral spot small or absent, the subapical bar often divided in two (sometimes lacking), the insect thus having an even blacker facies than *sayi* or *orbicollis*. Of these, only *tomentosus* and *orbicollis** were numerous in late July of 1944, and on them most of the following notes are based.

2. METHODS OF STUDY

Irondale is a hilly region from which the original timber was removed perhaps fifty years ago. Those areas which could be freed of glacial erratics and which were reasonably level, have been farmed (chiefly for grain). Other areas have been cleared for pasture and kept available for sheep and cattle. Less level land has been allowed to grow up again. The vegetation is typical Canadian zone, with hemlock, spruce, pine, paper birch, poplar, spiræa, sweet fern, sweet gale, mountain laurel, club mosses, bracken, and an abundant lichen flora on exposed rocks and tree trunks. Among the larger fauna are loons, whip-poor-wills, porcupines, groundhogs, skunks, red squirrels and chipmunks. Most of the glacial lakes contribute to the Burnt River system, deriving the name from the dark color of the water, due to leaching of iron ore from rock substratum and to solution of decaying coniferous and other xerophytic debris. Sphagnum is common and pitcher plants and sundew reach large size.

To attract *Nicrophorus*, small dead animals were placed at selected positions in a variety of ecological habitats. Each carcass was secured to a nearby stake by a two-foot length of fine steel wire, to make recovery easy (*cf.* Milne, 1928). The animals used

* Referred to as *N. pollinator* in Milne, 1928.

were chiefly deer mice (*Peromyscus*), with some house mice (*Mus*), shrews (*Blarina*), birds (robins, thrushes, sparrows, wrens, domestic turkeys, etc., as found dead) and snakes. In previous years larger carrion was tried, including groundhog (*Marmota*), skunk, dog, etc., but *Nicrophorus* was found to show little interest in carcasses too large for them to bury. For species observed at Irondale, a body the size of a robin is perhaps the limit.

In open fields, such as pastures or where hay had been cut, *N. tomentosus* and *marginatus* arrived to bury mice and snakes. Competition with ants was frequent and the carcasses deteriorated considerably before the beetles could get them buried. In leaf litter from birch and poplar, second growth woodland, *N. tomentosus* and *orbicollis* were quick to bury mice and birds. In coniferous duff the same species were somewhat slower in finding carrion. No activity was observed on mice placed in low, wet positions such as sedgy swales. Mice placed on particularly hard ground or on bare rock, were transported by the beetles to places where the soil was less packed and burial hence easier. Desiccation of carcasses by the sun did not have any noticeable effect on the interest in them shown by the beetles.

3. BEHAVIOR OF THE BEETLES

Nicrophorus exhibits a number of interesting behavior patterns. The beetles fly to the general vicinity of the carrion, apparently by smell (cf. Abbott, 1927a & 1927b; Milne, 1928). *Tomentosus* is particularly accurate in locating the body before alighting, buzzing through the bushes like a bumblebee. The resemblance to *Bombus* is enhanced by the golden body hair, the yellow inner surfaces of the elytra (which are held back to back over the midline) and the creamy cast to the flying wings. All *Nicrophorus* run about briskly, forcing their way through or under tangled vegetation. If disturbed, all but *tomentosus* are likely to either feign death, or run away a few feet to hide in grass roots. *Tomentosus* takes to its wings and may alight in a nearby bush, often standing on a slanting stem rather than the broader surface of a leaf. Pukowski (1933) describes a similar habit as part of the behavior of a lone *Nicrophorus* attracting a

mate, the beetle climbing a stone or plant, elevating the abdomen obliquely and extending it so much that the coriæ are visible. No indication of such was observed by the present authors, a lone *Nicrophorus* regularly getting to work on the burial task and continuing so engaged until a mate arrived.

After a beetle has arrived at a dead animal, it characteristically examines the body with palpi and antennæ and tests the size of the carcass by trying to move it. The "carrying" action is one of the most typical behavior patterns shown by *Nicrophorus*. Another activity closely related is that of "exploring" the surrounding soil for a suitable spot in which the body may be interred. A third procedure is to test the looseness of the soil by "plowing" it. All of these behaviors are energetic, and are shown by even a single *Nicrophorus*.

The carrying action of *Nicrophorus* demonstrates the strength of the beetles and the vigor with which they proceed with their task. To move a carcass, say forward in terms of a mouse's body, the beetle crawls under the head of the mouse, turns over on its back, and lifts the mouse bodily over itself. The mouse inches forward little by little, while the beetle slides slowly on its smooth back under the mouse until it reaches the posterior end. There it either emerges and runs around to the anterior end of the mouse again, or turns over on its feet to crawl under the mouse, the smooth dorsum of the beetle not disturbing the body. Such effort is very strenuous, and a rest period or an exploring interlude usually follows a few minutes of moving the carrion. A single beetle rests more than when a mate has arrived. A slight tug at the carcass usually stimulates it to renewed activity. When two beetles are operating one or the other is usually carrying the body while the mate explores or plows. No sexual difference in degree of activity could be noticed (*cf.* Wood, 1873; Furneaux, 1893; Pukowski, 1933). Both members of a pair were highly industrious under most circumstances. On level ground devoid of major obstacles, a pair of beetles may transport a full-grown mouse or shrew as rapidly as three or four feet per hour, and keep up this pace for as much as two and a half hours, the limit in every case observed being the distance necessary to reach sufficiently soft ground for burial use.

The exploring behavior was very distressing to the observers. After a shorter or longer period of work on a carcass, one or both members of a pair will suddenly leave the body and run away from it at the usual brisk pace. The beetles may go only a few feet (seldom less), or as much as a few yards, and in some cases (*tomentosus*) took to flight, only to return in a matter of minutes. A specimen of *N. tomentosus* with a broken elytral tip was observed to fly off and back again four times within an hour. Each time it flew out of sight. During the hour perhaps fifteen minutes work was done in carrying the mouse and in plowing in nearby soil, the remainder being either exploring the whole surrounding area (perhaps fifteen feet in diameter), or resting with head under a clump of grass, or absent altogether while away on a flight. This procedure persisted even after the specimen was joined by a mate, continuing until the carrion had been transported (mostly by the mate, in this instance), almost to the area selected for burial use.

The plowing procedure loosens the earth. The beetle uses its head as a plowshare or bulldozer, pressing into the earth perhaps the depth of its stout body below the surface, then forcing its way forward in an arc while maintaining its depth. The earth is forced upward and crumbles. Any roots encountered are either forced aside, or chewed through, but if numerous a new burial site is sought out. Before a final area is considered satisfactory, as many as twenty possible sites may be plowed and found unsuitable. The final area may be many feet away from the carrion, and the beetle(s) will alternately work on the carcass and run to the burial site to do another stretch of plowing. The route taken between carrion and burial site is usually fairly direct, and the body is carried along this line. How both members of a pair can agree on a site was not determined, nor was it at all clear how the beetles were able to keep the carcass moving so uniformly (few exceptions) in one direction. The contrast was very marked between the cooperation of *Nicrophorus* and the great wastage of effort among ants trying to carry a large food particle.

In a few instances, the beetle bait was placed on soft ground and the *Nicrophorus* buried it where it lay. In all instances,

however, the burial procedure was a localization of the plowing action. The beetles plowed *under* the carrion, entering at one side (or end) and emerging at the other, only to turn about and complete the shuttling action. On each emergence at the side or end of the carcass, a sizeable amount of earth was forced up, to accumulate in a loose pile all around the body. Gradually the earth from below the carrion was displaced to the side and the carcass settled into the ground. A continuation of the same activity gradually drops the body below the surface of the ground, and the procedure is continued until as much as two inches of earth are over the carcass. The body is usually let into the ground at a steep angle. Not only the earth under the carrion, but also that within a few inches of it is plowed. Closer to the body the ground is plowed to a greater depth. In its final site, a chamber is cleared of earth below and to one side from the body. In the chamber *Nicrophorus* remains after burial. The chamber may be as much as two and a half inches long, an inch wide and deep, and the walls are left packed in the original condition of the earth, so that cave-ins are unlikely. Burial is usually completed in five to eight hours, although the beetles will continue for days if obstructions slow their work. *Nicrophorus* usually remain with the carrion at least for many days (*cf.* Hatch, 1927b; Milne, 1928; Pukowski, 1933; Leech, 1935).

There seems to be a relationship between the size of the carrion, the size of the *Nicrophorus* species and the number of pairs which can work in burying it. A full sized robin (in juvenile plumage) was handled by a pair each of *N. orbicollis* and *tomentosus*. A thirty-inch garter snake was buried by two pairs of *N. tomentosus* and one of *marginatus*. In one instance a full-grown deer mouse was interred by two pairs of *N. tomentosus*. In all other instances only a single pair of a single species did the work. Additional specimens of *orbicollis* arriving at a piece of carrion where a pair were at work, usually crawled under the body, only to emerge (promptly!) pursued by one of the original pair. Several rough and tumble fights were witnessed in which the newcomer resisted briefly the attack of the original "owner." *Orbicollis* coming to carrion where *tomentosus* was at work usually drove the smaller species away. *Tomentosus* coming to

a carcass being carried or buried by *orbicollis* usually left without any indication of expulsion. *Tomentosus* coming where *tomentosus* were already at work sometimes helped awhile before leaving, in only one instance (see above) remaining until the body was completely interred. Thus *tomentosus* would seem to make up in small size, greater numbers (see below) and more sociable reactions for its inability to compete physically with the larger species. *Orbicollis* becomes quite excited over expelling a competitor and stridulates very audibly by rubbing the upper surface of the abdomen against the under surface of the elytra (*cf.* Morley, 1902). This same stridulation is observed when a pair mate (3 to 4 seconds; *cf.* Pukowski, 1933), or when an obstruction continues to bar the way in moving a carcass. These were the only occasions and the only species in which such noises were noted. Pukowski (1933) indicates that pairs working on a carcass keep in contact with each other by alternately emitting "zirping" sounds.

Obstructions may be of a variety of types. Naturally encountered are situations where roots, stems, leaf petioles, etc., are sufficiently anchored at both ends as to restrict an opening through which the beetle is attempting to move the carrion. The beetle discovering such an obstacle usually tries first to force it out of the way, getting head and pronotum under the restraining strand, feet in the vestiture of the carrion, and crawling ahead. Many obstructions can be stretched sufficiently by this method to open a suitable passage for further progress of the carcass. When force proves inadequate, the beetle may settle down on the restraining piece and laboriously chew it through. Often periods of chewing are alternated with episodes of drawing and pushing at the carcass or strand, the chewing frequently having weakened the obstruction sufficiently to let it give. When the obstacle proves too resistant to such treatment, soil is plowed from under the carcass and the needed space obtained in this way.

Obstructions provided experimentally were usually very irritating to the beetles but in no case did they leave permanently. String tied to the leg or tail of a mouse was the commonest form of restraint, and one which could be overcome by gnawing the string until it broke under strain. Fine steel wire was an in-

superable difficulty. A carefully placed piece of rock, supported partly on the ground and partly on the body of a mouse, proved less of a problem. Although the rock weighed several pounds, the pair of beetles working together were able to lift the rock where it rested on the mouse sufficiently to push the carrion free of its pressure and restraint.

One experimental situation gave a good demonstration of the beetles' behavior. A mouse laid out on fairly soft ground had a string tied to one hind leg, the opposite end of the string being fastened to a stake close to the mouse but in such a way that the string was almost vertical and held the leg clear of the ground. A pair of *N. orbicollis* proceeded to bury the mouse. They did a fine job, the head of the mouse finally hanging almost vertically downward into the hole the beetles had excavated. The hind leg continued to be supported in its original position. The beetles cleared away the earth until there was none below the head and shoulders of the mouse for a distance equal to the thickness of a beetle, and a space was also clear all around the mouse so that it hung by its one leg over a sizeable, cup-shaped hole. With much stridulation and rotation of the mouse around and around over the hole, the beetles failed to go vertically upward to the supporting string. Every move in this direction ended in a trip out the length of the mouse's tail, to see that it was free. It was, but the traffic became so heavy and the mouse so "ripe" that the skin rolled off the tail distally like a glove finger. Finally the beetles gnawed the tail off the mouse, severing it at the root. Almost at once they found the supporting string, and after a few abortive attempts to free the foot, one of the *Nicrophorus* settled down to the task of gnawing it through. When the string gave way, the mouse collapsed in a heap into the bottom of the hole prepared for it, and burial was completed uneventfully within half an hour.

Pukowski (1933) indicates that the beetles prepare a conical hole below the carrion, always smaller than the body, and fold the carcass as they draw it into the pit. The episode just described would seem to indicate that *Nicrophorus* continue to enlarge the hole for the carcass until it has been sunk to their satisfaction, and that a conical hole and consequent folding may

be merely economy of effort. When carrion has considerable length, as for example a snake, no folding was observed by the present authors. The snake was let into the ground to a depth of nearly two inches all along its length (except for the tail), so that it was buried horizontally, in approximately the attitude occupied previously on top of the earth. It is true that in the case of snakes, burial advanced rapidly in the region from head to anus, the tail being left out in the air for nearly twenty-four hours after the remainder of the carcass was well under the surface. The tail, with its smaller supply of food materials, was obviously of much less interest to the beetles, forming chiefly an obstruction to satisfactory burial. In several instances the last few inches of a snake's tail was chewed off, and the postanal remainder pulled into the ground after putrefaction had rendered it more plastic.

Heavy rain obstructed burying beetles much less than had been expected. On several occasions *Nicrophorus* had begun to bury bait placed on level, hard ground, when torrential downpours drove the observers to nearby shelter. From the cabin the bait could be seen almost or quite covered by water, sometimes to a depth of an inch. No sign of the beetles was noted, yet within fifteen minutes after the rain slackened enough for the ground to drain off, the insects were busy in the wet earth, excavating, plowing and tugging the carcass into their cavity.

The observers' concern over the seeming desertion of the bait whenever *Nicrophorus* went into an exploring episode, suggested another experiment. As indicated above, the beetles frequently explore a very sizeable area before returning to the carcass. There is no indication, however, that there is ever any difficulty in finding the carcass again, since the beetles often return to it in an almost straight line from a distance of a yard or two. On several occasions, duplicate baits were tried, being mice of approximately equal size and state of preservation, placed a foot apart on even terrain. A *Nicrophorus* would come to one, test it for size, then explore the surrounding ground for a suitable burial site. During the exploration the second mouse was usually discovered. Almost without exception, the beetle examined the duplicate bait without attempting to carry it, then hurried back to the mouse

previously discovered. In no case observed did the beetle(s) desert the first bait in favor of the second. The same type of experiment was tried on pairs which were busy burying a relatively fresh mouse. A similar (or more odoriferous) mouse was placed where they would surely find it during exploration trips. In no case did the beetles desert the first-found carcass to more than examine the second. It was quite obvious that the extra carrion so nearby was a source of great distraction, but the recognition of one body as distinct from another was most marked.

In only a few instances did *Nicrophorus* show any indication of feeding on the carrion (*cf.* Furneaux, 1893; Lutz, 1921; Steele, 1927; Milne, 1928). Usually the beetles seemed to be in a hurry to get the carcass interred. During daylight the need for rapid burial was great, since blowflies came in considerable numbers, laying living larvæ if unmolested for a few minutes. The brisk activities of the beetles and the frequent jerky movements of the carcass have a deterrent effect on flies of some types (including blowflies) but where obstacles prevented beetles from quickly getting the carrion under ground during daylight hours, it was obvious that little of the carcass would be available for other than dipterous larvæ. In many instances the beetles seemed to realize this, and failed to complete burial. In some cases *Nicrophorus* left fly-ridden carcasses sunk below the level of the ground, covered by perhaps a quarter of an inch of loose earth. A few days later such carrion was a squirming mass of fat fly larvæ. Rapidly buried bodies, on the other hand, are remarkably free of dipterous contamination. This may well be due to the preference shown by beetles for operations in twilight, at night or on cloudy (even rainy) days (*cf.* Abbott, 1927b) or an active eating of young maggots by the beetles (noted on a few occasions; *cf.* Steele, 1927; Leech, 1935).

In one instance of *Nicrophorus* feeding, one member of a pair took time off to investigate a small hole in the abdomen of a "ripe" mouse, while the mate was busy excavating under the carcass. For perhaps five minutes the feeding beetle worked into the hole, until head and pronotum were inside the abdominal wall. The viscera were explored rather superficially since the position of the head could be discerned at all times by the moving

elevation it produced in the mouse's skin. It was the observers' opinion that the beetle was drinking rather than eating. Prior to this feeding action, small flies had found the hole in the mouse's abdominal wall a very interesting region, and considerable moisture seemed to be present. After the beetle left the hole, there was no liquid visible and no flies were attracted to the area. During feeding, several blowflies ran against the posterior end of the beetle, and were kicked away by violent movement of the posterior legs. This kicking of molesting flies and ants seems a common reaction in *Nicrophorus*.

Nicrophorus apparently discovers carrion entirely by smell, while ants frequently locate freshly killed mice, seemingly as part of routine foraging operations. Often ants had removed the lips and nosetip of the rodent (the first part to be attacked in all instances observed) before *Nicrophorus* arrived, but on warm days (or nights) the beetles began to arrive within an hour or less. Typical of the speed with which *Nicrophorus* gather at a mouse is the following record made between six and ten o'clock one warm evening:

- 5:30 P.M. Freshly killed mouse laid out in birch leaf litter.
 6:05 ♀ *N. tomentosus*.
 6:07 ♂ *N. tomentosus*.
 6:19 ♂ *N. tomentosus*.
 6:38 ♂ *N. orbicollis*.
 6:40 ♂ *Silpha americana*.
 7:33 ♀ *N. tomentosus*.
 8:02 ♀ *N. orbicollis*.
 8:13 ♂ *N. orbicollis*.
 8:36 ♂ *S. noveboracensis*.
 8:41 ♀ *S. americana*.
 8:47 ♀ *N. orbicollis*.
 9:00 ♂ & ♀ *S. noveboracensis*.
 9:40 carabid beetle.
 9:50 ♂ *N. tomentosus*.
 10:00 Took in mouse for the night.

Thus in four hours, nine *Nicrophorus* arrived, of which approximately half were males. The sex ratio is remarkably close to 1:1. Of twenty-two specimens of *N. orbicollis* collected in the sequence

in which they arrived (no selection), ten were females. Of forty-one *N. tomentosus* collected in the same way (and during the same time limits), twenty were males. Other observers confirm the sex ratio (*cf.* Wood, 1873; Leech, 1935). The ratio of twenty-two *orbicollis* to forty-one *tomentosus* is a very good value to indicate the relative abundance of the two species in deciduous woodland. In the sample catch cited above in chronological order, the proportion of *N. tomentosus* is unusually low. Some may have been driven off by *N. orbicollis* between arrival of *orbicollis* and the frequent visits of the observers. Mosquitos made more constant supervision too uncomfortable.

Another indication of the frequency with which *Nicrophorus* come to carrion was afforded by an unintentional experiment. Usually the observers placed all bait which was to be saved for the morrow in a glass jar to be kept overnight on ice. On one occasion a relatively fresh mouse was tossed casually into a butterfly net, the net folded on itself a few times, and left standing outside the cabin over night. In the morning two *N. tomentosus* were collected on the outside of the net just over the mouse inside. Holes had been chewed through the net thicknesses to allow entry of five other *Nicrophorus*, two *orbicollis* which had reached the mouse, one *orbicollis* nearby in a fold of the net, and two *tomentosus* in still other folds. Concern over the damage done to the net precluded observations on how the beetles might have gone about burying a carcass under such conditions.

The authors have been unable to identify the sex of *Nicrophorus* in the field without examining the genitalia—a procedure which is accomplished more satisfactorily on an anæsthetized specimen. Records for *N. orbicollis* were kept, however, to determine if there were any clue to sex in the size of the specimens. Ten male and eleven female *orbicollis*, measured freshly killed and extended, form the basis of study. Since the telescoping of the abdomen provided an independent variable, measurements were made from the most anterior part of the head capsule to the elytral apex. For the ten males there was a variation in this measurement from 14 to 22 mm., mean 19.6 mm., with a standard error of 2.7 mm. or approximately 14%. For the eleven females the variation was from 16 to 22 mm., mean 18.5 mm., with a

standard error of 2.2 mm., or nearly 12%. Since the difference between the means is only 1.1 mm. (about 6%), the authors were unable to use size for sex recognition. A small male and a large female, or vice versa, were encountered more frequently than two large or two small specimens.

Due to the preference shown by *Nicrophorus* for work in the shade or at twilight or night, difficulties were experienced in obtaining photographic records. So as to have beetles available to photograph when the light was good, attempts were made to imprison photogenic specimens in glass jars with a little earth. If the earth were moist, isolated specimens burrowed into it and were active the following day, showing little agitation over their confinement and taking on the burial of any mouse provided them as soon as liberated quietly beside it. However, the beetles became very hungry when kept over night, and unless maintained in solitude, resorted to cannibalism. Specimens killed by their fellows were ripped apart most ruthlessly, head from pronotum from remainder of thorax from abdomen, and each part cleaned of viscera. The victors frequently lacked tibiae, antennae, sometimes whole legs and elytra, demonstrating the ferocity of the battles. *Onthophagus*, histerids and larvae of *Silpha* seemed able to escape such attacks, but adult *Silpha* and *Nicrophorus*, as well as other staphylinids and scarabæids (e.g., *Geotrupes*) were destroyed by hungry *N. orbicollis* and *tomentosus*. When specimens were confined without food for more than a day, they became sluggish and often died. Pukowski (1933) mentions *N. germanicus* attacking adult *Geotrupes silvaticus*, capturing them at horse dung, seizing them in the legs and mandibles and devouring the viscera. *Nicrophorus* rolls over on its back or one side while eating such prey.

4. RELATED OBSERVATIONS

Among other species frequenting, but not burying, small carcasses, the following beetles were most common:

Staphylinidæ: *Silpha surinamensis* Fab., *S. lapponica* Hbst., *S. inaequalis* Fab., *S. noveboracensis* Forst. and *S. americana* L., *Staphylinus fossator* Grav., *Ontholestes cingulatus* Grav. and *Creophilus villosus* Grav.

Histeridæ: unidentified—at least three species, probably different genera.

Scarabæidæ: *Geotrupes blackburnei* Fab., *Onthophagus hecate* Panz., *O. orpheus* Panz., *O. nuchicornis* L.

Of these *Silpha noveboracensis* and *americana* and *Onthophagus hecate* were most numerous, coming both night and day, particularly to carrion which had deteriorated considerably. *Staphylinus fossator*, *Ontholestes cingulatus* and *Creophilus villosus* came to similar carcasses but chiefly in daylight hours. All of these species chewed at the bait. No evidence was obtained as to the food of the histerid species. None of these beetles was driven off by *Nicrophorus*, but only the histerids and *Onthophagus* remained if the carcass was buried.

Larvæ of *Silpha* usually come in small numbers to deteriorated carrion, and can be found many feet away heading toward the carcass with remarkable accuracy. The larvæ and adults of *Silpha* walk with a rapid, jerky movement. In the adults the jerks are more pronounced, possibly because the legs are longer. *Silpha* larvæ roll up like terrestrial isopod crustaceans ("sow bugs, pill bugs") and feign death, but the adults run away if disturbed.

Most of the carrion beetles (and dung beetles) carry a number of mites. *Nicrophorus* usually have less than twenty (*cf.* Leech, 1935). On arrival at carrion, many of the mites leave the beetles and may be found running about on the carcass and nearby ground. They hurry around on the body of the beetles and appear to share any agitation shown by the insect. Thus when the beetle is disturbed, the mites move much more extensively and leave the beetle much more frequently. The arrival of another beetle or irritation shown over some obstacle to burial is enough to greatly excite the mite population. The beetles were never seen to show any reaction to the presence or position of the mites, but it was noted also that the mites did not crawl out on the antennæ of the insects, although they ran over the mouthparts, dorsum, venter and leg bases. Schaupp's (1881) notes are interesting in suggesting a relationship between mites and the death of *Nicrophorus* pupæ.

Pukowski (1933) and Leech (1935) have followed in great

detail the later phases of the life history, subsequent to burial of the carcass. The present writers have not had opportunity to repeat many of these observations. They did note, however, that carcasses were cleaned fairly well of hair or feathers and worked into a compact ball, kept free of collected moisture, the skin remaining in fair condition while the tissues became a slate-gray, pasty mass, of a consistency similar to rotting dung. To see some of the later stages in the life cycle, two mice were laid on the top of four inches of earth and forest litter packed into a granite dish. Within a day, both mice were buried by pairs of *N. tomentosus*, and the dishful of carrion and insects was screened and carried home to Pennsylvania. Perhaps due to the agitation of the trip, the *Nicrophorus* came out of the ground and were observed running about over the soil, fluttering their wings and seeking an exit. Two of the four beetles (a pair) were caught and removed, and the remaining pair left to minister to any young they might have on the way. Soil moisture was maintained by occasional watering. The two beetles were seen running around a few times more, but on each occasion they returned into the earth. After two weeks one beetle was noticed on top of the ground, dead and eviscerated. The pan of carrion and earth was turned out on a paper. One mouse had dried to a hard mass. The second was in much better condition, and on it were two fat yellow larvæ of *N. tomentosus*, so distended with food that their intersegmental membranes were more conspicuous than the brown sclerites, and almost helpless to roll over and crawl away. The other parent (♀) was found dead among the earth. About two dozen fly puparia were among the soil particles, probably from the dried mouse. No further observations were made and the specimens were preserved for reference.

The foregoing observations were made during and between shots with the 16 mm. motion picture camera. A visual record in Kodachrome was obtained, somewhat over 600 feet in length, showing the carrying and plowing behaviors, the burial of several mice, the exhumation of mice and a snake, close-ups of *N. tomentosus* adults and larvæ, of *N. orbicollis*, including some footage made at night to the hum of mosquitoes while *N. orbicollis* chewed through the string which held up the leg of a mouse. The present

notes on the burial behavior of *Nicrophorus* should fill in gaps left in the excellent work of Pukowski (1933) and Leech (1935) and with the film, allow entomologists more widely to become acquainted with the activities of this interesting genus.

ANNOTATED BIBLIOGRAPHY

- ABBOTT, C. E. 1927*a*. Experimental data on the olfactory sense of Coleoptera, with special reference to the Necrophori. *Annals Ent. Soc. Amer.* 20: 207-216. Indicates olfactory sense located all over body of *Nicrophorus*; studied *N. americanus*, *orbicollis* and *tomentosus* from Md. in June.
- . 1927*b*. Further observations on the olfactory powers of the Necrophori. *Ibid.*: 550-553. Same in *orbicollis* in Wis. (July)
- . 1937. The necrophilous habit of Coleoptera. *Bull. Brooklyn Ent. Soc.*, 32: 202-204. Indicates an obvious ecological succession of beetles, the kind of carrion determining the numbers and species involved.
- BALDUF, W. V. 1935. The bionomics of entomophagous Coleoptera. (J. S. Swift Co., Inc.) Pp. 68-75. An excellent summary of the literature, particularly the work of Pukowski.
- BELL, PROF. 1873. A glimpse of insect life. *Can. Ent.* 5: 94-95. Observed adult *Nicrophorus* removing maggots from a dead dog.
- CLARK, C. U. 1895. On the food habits of certain dung and carrion beetles. *Jour. N. Y. Ent. Soc.* 3: 61. Mentions *Nicrophorus* feeding on maggots.
- DAVIS, W. T. 1915. *Silpha surinamensis* and *Creophilus villosus* as predaceous insects. *Jour. N. Y. Ent. Soc.* 25: 150. Mentions *Nicrophorus* feeding on maggots from woodchucks and squirrels.
- DUNCAN, C. D. AND G. PICKWELL. 1937. The world of insects. (McGraw-Hill Book Co.) Pp. 194. Indicates that *Nicrophorus* larvæ develop in a carcass before bacteria cause serious decomposition.
- FABRE, J. H. 1899. *Souvenirs entomologiques*. VI. Pp. 113-153.
- FOWLER, W. 1912. Coleoptera—General Introduction, Cicindelidæ and Paussidæ. *Fauna Brit. India* 1912: 12, 24. Discusses olfactory pits on antennæ, and indicates *Nicrophorus* as typical of temperate climates.
- FURNEAUX, W. 1893. The outdoor world. (Longmans, Green & Co.) Pp. 141-143. Indicates that female *Nicrophorus* is first to settle on carcass, that male flies about, then both gorge selves on carrion, after which male buries carcass without help of female.
- HATCH, M. H. 1927*a*. Studies on the Silphinae. *Jour. N. Y. Ent. Soc.* 35: 331-371. Primarily a taxonomic paper, indicating *Nicrophorus* as the spelling used by Fabricius in erecting the genus.
- . 1927*b*. Studies of carrion beetles of Minnesota, including new species. *Univ. Minn. Agric. Exp. Sta. Tech. Bull.* 48: 3-7.

- . 1940. Observations on Silphinae, with a note on intraspecific variations and their designation. *Jour. N. Y. Ent. Soc.* 48: 233-244.
- JAKUES, H. E. 1915. The fish feeding Coleoptera of Cedar Point. *Ohio Nat.* 15: 525-528. Indicates *Necrophorus* feeding on fish washed ashore.
- LEECH, H. B. 1935. The family history of *Necrophorus conversator* Wlk. *Proc. Ent. Soc. B. C.* 31: 36-40. The most complete life history study of a North American species.
- LUTZ, F. E. 1921. *Fieldbook of insects.* (G. P. Putnam's Sons.) Pp. 295-296. Cites *N. americanus* as preferring reptiles, but indicates no burying beetles came to any bait set out under experimental conditions.
- MILNE, L. J. 1928. Notes on Silphidæ in Haliburton County, Ontario. *Can. Field Nat.* 42: 43. Earlier observations on burying behavior.
- MORLEY, R. L. 1902. Notes on stridulation. *Ent. Mo. Mag.* 38: 249-250. Indicated that abdomen was rubbed on elytra to produce noise, and coxæ play no part in *N. moratorium*.
- MOTTER, M. G. 1898. A contribution to the study of the fauna of the grave. *Jour. N. Y. Ent. Soc.* 6: 201-231. Indicates no *Necrophorus* on disinterred corpses (*cf.* Wood, 1873).
- PUKOWSKI, ERNA. 1933. Oekologische Untersuchungen an *Necrophorus* F. *Zeits. Morph. Okol. Tiere* 27: 518-586, 25 figs., refs. The most complete account of the life history of European species of *Necrophorus*, including references to the European literature.
- SCHAUPP, F. G. 1881. Description of the larva of *Necrophorus tomentosus* Web. *Bull. Brooklyn Ent. Soc.* 4: 37-38. Indicated that mites killed 50 per cent of *Necrophorus* pupæ by sucking them dry.
- SELOUS, C. F. 1911. A preliminary note on the so-called carrion-feeding Coleoptera. *Ent. Mo. Mag.* 47: 86-89. Beetles flew into wind, walking last few feet to carrion, dragged carcasses to softer earth. Not convinced that *Necrophorus* are feeders on carrion, probably predators.
- STEELE, B. F. 1927. Notes on the feeding habits of carrion beetles. *Jour. N. Y. Ent. Soc.* 35: 77-81. Indicated *N. orbicollis* and *tomentosus* ate maggots from a woodchuck, and preferred maggots to carrion.
- THOMSON, SIR J. A. 1935. *Biology for everyman.* (E. P. Dutton.) Vol. 2: 866-867. Brief summary of life history.
- WOOD, J. G. 1873. *Insects at home.* (Wm. Rutter.) Pp. 86-93. Indicates *Necrophorus* attack poorly interred human bodies in Russia. Found sex ratio about 1:1. Other observations correspond to those of Furneaux, but more extended.